EVOLUTION

INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

Vol. 26 *September 1972* **No. 3**

CONTENTS

Effects of Population Density on the Frequency-dependent Selection in the Esterase-6 Locus of *Drosophila melanogaster*. KEN-ICHI KOJIMA AND SHIU LAN HUANG 313

Maintenance of Chromosomal Polymorphism in a Population of *Drosophila pseudoobscura*: Viability under Crowded and Uncrowded Conditions. MARVIN DRUGER AND RICHARD P. NICKERSON 322

Courtship Interaction in the Semispecies of *Drosophila paulistorum*. SUSI KOREF-SANTIBAÑEZ 326

Selection and Stability in the Complex Polymorphism of *Moraba scurra*. JOHN R. G. TURNER 334

Random vs. Non-random Mating in the Sulfur Butterflies, *Colias eurytheme* and *Colias philodice* (Lepidoptera: Pieridae). ORLEY R. TAYLOR, JR. 344

Evolution in Mixed Populations of *Tribolium*. PETER S. DAWSON 357

Competition between Metal Tolerant and Normal Plant Populations on Normal Soil. SHEILA C. A. COOK, CLAUDE LEFÉBVRE, AND THOMAS MCNEILLY 366

Pollination Biology of *Nemophila menziesii* (Hydrophyllaceae) with Comments on the Evolution of Oligolectic Bees. ROBERT WILLIAM CRUDEN 373

Rapid Population Differentiation in a Mosaic Environment. II. Morphological Variation in *Anthoxanthum odoratum*. R. W. SNAYDON AND M. S. DAVIES 390

The Reproductive Biology of *Rhus integrifolia* and *Rhus ovata* (Anacardiaceae). DAVID A. YOUNG 406

Fertile Glumes in Primitive Cultivated Wheats. G. M. WRIGHT 415

DNA Content in Relation to Phylogeny of Selected Boreal Forest Plants. M. H. EL-LAKANY AND JANET R. DUGLE 427

Evolutionary Implications of *Zahnreihen*. ROBERT DEMAR 435

Numbers of Bird Species on the California Islands. DENNIS M. POWER 451

The Evolution of the Use of Tools by Feeding Animals. JOHN ALCOCK 464

Some Functional Aspects of Molar Evolution. P. M. BUTLER 474

Book Reviews

Primate Societies: Group Techniques of Ecological Adaptation. BENJAMIN B. BECK 484

Theoretical Aspects of Population Genetics. JACK LESTER KING 485

Vertebrate Paleozoology. DAVID BARDACK 487

Announcement 333

PUBLISHED QUARTERLY

BY THE SOCIETY FOR THE STUDY OF EVOLUTION

ISSUED NOVEMBER 14, 1972

NUMBERS OF BIRD SPECIES ON THE CALIFORNIA ISLANDS

Dennis M. Power[1]
Department of Ornithology, Royal Ontario Museum and Department of Zoology, University of Toronto, Toronto, Ontario, Canada

Received October 22, 1971

Variation in bird species diversity on islands is related to island area in a simple way. Correlations between numbers and area have been found for birds of the West Indies, East Indies, Madagascar and the Comoro Islands (Preston, 1962), and for a number of other archipelagos. In reality of course the situation is more complex. Area is often correlated with environmental diversity, a complex collection of factors which frequently exerts a more direct effect on species diversity than area itself (MacArthur, 1964; Watson, 1964). It is likely also that interactions with other species, both in competition and predation, figure predominantly (Crowell, 1962; Grant, 1966; Lack, 1969). And there are distance effects on rates of immigration and extinction such that those islands that are isolated tend to have fewer species than those near a source of propagules (MacArthur and Wilson, 1967).

There have been two basic approaches to the study of variation of insular diversity. One is to consider numbers of species as a dependent variable and factors such as area, habitat diversity, topography, and distance from the nearest mainland or other islands as independent variables, and by multiple regression or similar analysis determine the components which explain statistically most of the variation in numbers. This has been done for numbers of land and freshwater bird species on various islands of the Moluccas, Melanesia, Micronesia, and Polynesia (MacArthur and Wilson, 1963), the islands of the Aegean Sea (Watson, 1964), the Solomon Islands (Greenslade, 1968), the islands of the East Indies, East-central Pacific Ocean, and West Indies (Hamilton et al., 1964), islands of the Gulf of Guinea (Hamilton and Armstrong, 1965), and the Hawaiian and Galápagos archipelagos (Hamilton and Rubinoff, 1967). The other approach is to test predictions from the equilibrium theory of MacArthur and Wilson (1963, 1967) which accounts for number of species on a single island by balancing immigration rate with extinction rate and considers factors such as area and isolation that affect these rate functions. Although the equilibrium theory provides a realistic model that takes into account the dynamic properties of an insular biota, the need still exists to isolate specific factors operating in different situations. It is desirable therefore to continue to design multiple regression models that are somewhat more refined when conditions permit and that take into account new independent variables when data are available. Multiple regression, of course, can only demonstrate statistical relationships, but from these one hopes to interpret causal relationships as well. Results from statistical procedures such as this are naturally subject to some data-dependent error and therefore require knowledgeable interpretation, just as is true with any analytical tool.

The present study is an analysis of numbers of land bird species breeding on islands off the coast of southern California and northwestern Baja California, Mexico (Fig. 1). The islands are situated along a relatively extensive coastline and variation in bird species numbers on coastal islands has received little attention in the past. In addition, one of the advantages of studying

[1] Present address: Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, California 93105.

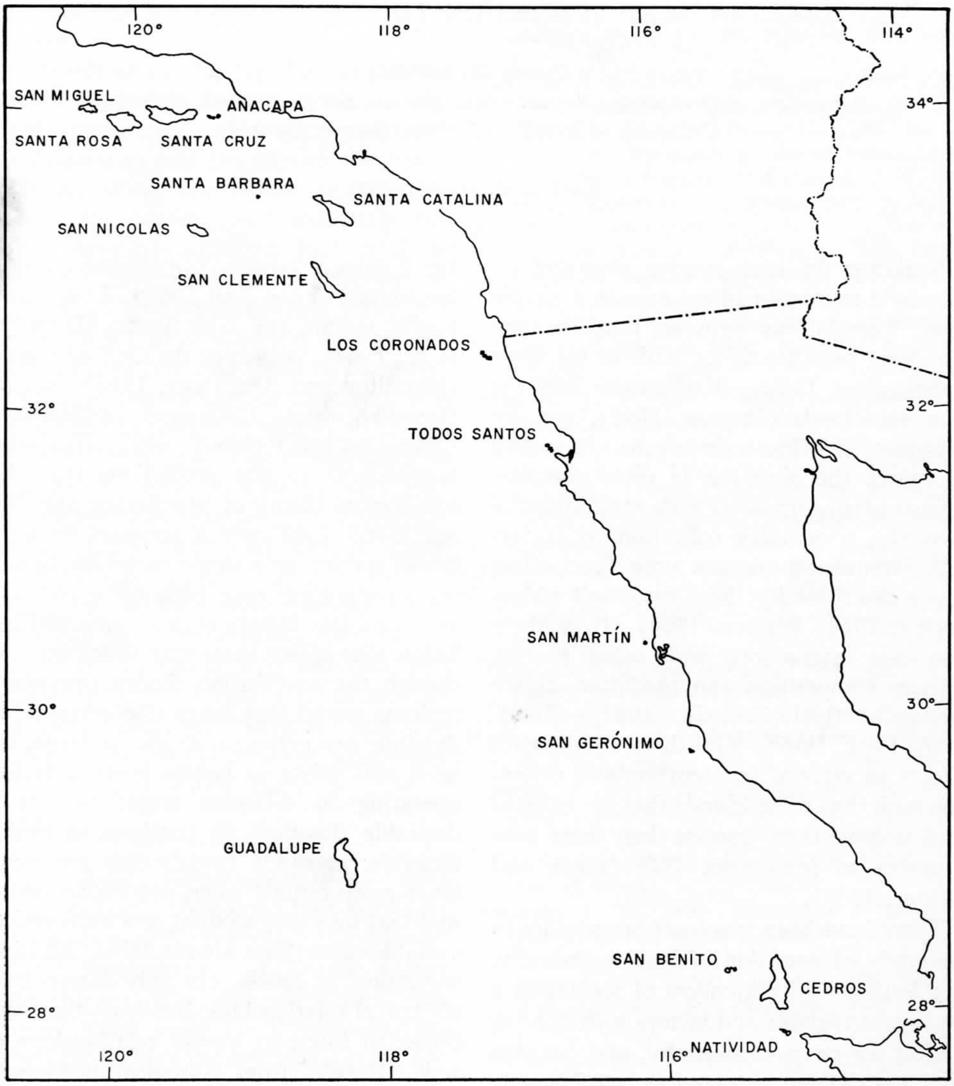

FIG. 1. Map of the California Islands.

the California Islands is that they have received the attention of a number of naturalists in the last 100 years. Not only is the bird fauna relatively well known, but so is the flora, an obviously dominant component of habitat diversity. A model in the form of a path diagram is presented that relates bird species diversity to plant species diversity and isolation as direct factors, and area and latitude (representing changes in rainfall) as indirect factors.

ORIGIN OF THE BIRD FAUNA

The geologic history of the California Islands has been summarized by Thorne (1969) and considerable recent information is given in the papers of a symposium edited by Philbrick (1967). Guadalupe Island, some 165 miles from Baja California, is the only true oceanic island. It is volcanic in origin and rises 15,000 feet from the sea floor. The oldest lava flow is estimated at

TABLE 1. *Untransformed data.*[1]

Island	*B*	*A*	*E*	*L*	*P*	*I1*	*I2*	*I3*	*I4*	*I5*	*I6*	*I7*	*I8*	*I9*
San Miguel	10	14	830	34.0	190	26	3	217.3	12	10	8	0.531	0.502	0.485
Santa Rosa	22	84	1560	34.0	340	27	3	202.4	12	8	7	0.396	0.339	0.333
Santa Cruz	32	96	2470	34.0	420	20	5	193.1	12	8	7	0.473	0.446	0.440
Anacapa	16	1.1	930	34.0	70	13	13	192.9	10	8	7	0.624	0.595	0.588
San Nicholas	10	14	830	34.0	190	26	3	177.5	12	8	6	0.902	0.832	0.819
Santa Barbara	13	1.0	635	33.4	40	38	24	173.9	10	8	6	0.824	0.796	0.782
Santa Catalina	28	75	2125	33.3	392	20	20	162.6	13	8	6	0.856	0.782	0.764
San Clemente	23	56	1965	32.9	235	49	21	156.5	12	8	6	0.881	0.830	0.813
Los Coronados	13	1.0	670	32.4	83	9	9	168.1	14	12	5	0.717	0.762	0.790
Todos Santos	14	0.5	315	31.8	72	3	3	173.6	14	13	7	0.547	0.536	0.496
San Martín	4	0.9	470	30.5	62	3.5	3.5	199.6	15	13	8	0.731	0.702	0.683
San Gerónimo	2	0.2	130	29.8	4	6	6	221.0	15	14	8	0.815	0.795	0.749
Guadalupe	12	98	4600	29.0	163	165	165	243.5	16	16	9	1.000	1.000	0.964
San Benito	7	2.5	660	28.3	39	44	19	278.1	14	13	10	0.873	0.896	0.910
Cedros	12	134	3950	28.2	205	14	10	278.7	13	13	10	0.760	0.760	0.738
Natividad	5	2.8	490	27.9	42	5	5	302.0	13	13	10	0.675	0.675	0.662
Mean	13.94	36.3	1414.4	31.72	159.2	29.3	19.5	208.80	12.9	10.8	7.5	0.7253	0.7030	0.6885
S.D.	8.50	46.1	1310.8	2.37	132.2	38.9	38.5	45.01	1.7	2.8	1.6	0.1719	0.1766	0.1762

[1] See text for explanation of variables.

about seven million years old. All of the native bird species probably arrived over water. The remaining islands are truly coastal, appearing as the emergent tips of mountain ridges that continue from the continent. There have been various periods of uplift, submergence, and continental and inter-island connections dating from Cretaceous times. The latest connection between the continent and the northern-most islands—namely, San Miguel, Santa Rosa, Santa Cruz, and Anacapa—was in the mid-Pleistocene, perhaps half a million years ago. By the Illinoian the connection was severed. During the Iowan or lower Wisconsin glacial stages from about 11,000 to 20,000 years ago, lowered sea levels likely permitted inter-island but not island-mainland connections. San Nicholas and Santa Barbara islands were totally submerged during the late Pleistocene. Connections of San Clemente and Santa Catalina islands with the mainland probably did not occur during the Pleistocene. The islands off the coast of Baja California, with the possible exception of San Benito, were probably connected to the peninsula during the lowest sea level of the Wisconsin glacial stage. Shortly after the Pleistocene there appears to have been a marked xerothermic period.

Even though past connections suggest that many of the bird species on the higher islands could be Pleistocene relicts, distributional and morphological evidence suggests that much of the avifauna arrived over water in more recent times (Johnson, 1972). In addition, Diamond (1969) suggests that turnover rates are high and that 16 to 60% of the avifauna on the islands from Los Coronados northwards could have arrived in the last 50 years. On the islands north of Los Coronados only phenetically distinct populations of the Scrub Jay (*Aphelocoma coerulescens*), the Horned Lark (*Eremophila alpestris*), and the Orange-crowned Warbler (*Vermivora celata*) appear to be relicts. The avifauna of Guadalupe Island appears to be older however as a number of phenetically distinct populations occur there.

EXPLANATION OF VARIABLES (TABLE 1)

Numbers of bird species (B).—The numbers of breeding or summer resident species of land birds were obtained from Grinnell and Miller (1944) for the islands

TABLE 2. *Correlation coefficients between variables. Lower triangular matrix for untransformed data, upper for log-transformed data.*[1]

	B	*A*	*E*	*L*	*P*	*I1*	*I2*	*I3*	*I4*	*I5*	*I6*	*I7*	*I8*	*I9*
B		**0.64**	**0.70**	**0.60**	**0.84**	0.42	0.19	**–0.49**	–0.47	**–0.66**	–0.48	–0.30	–0.34	–0.32
A	**0.57**		**0.91**	0.12	**0.85**	**0.61**	0.25	0.05	–0.08	–0.31	0.07	–0.07	–0.14	–0.13
E	040	**0.91**		0.08	**0.82**	**0.66**	0.49	0.03	–0.12	–0.24	0.04	0.05	0.01	0.02
L	**0.60**	–0.06	–0.19		0.44	0.12	–0.28	**–0.81**	**–0.64**	**–0.85**	**–0.79**	–0.41	–0.48	–0.47
P	**0.86**	**0.75**	**0.53**	0.48		0.41	0.03	–0.27	–0.25	**–0.50**	–0.24	–0.28	–0.34	–0.31
I1	0.06	0.39	**0.66**	–0.19	0.10		**0.68**	0.01	–0.16	–0.24	–0.02	0.32	0.27	0.28
I2	–0.01	0.36	**0.66**	–0.30	0.00	**0.96**		0.08	0.12	0.17	0.08	**0.64**	**0.64**	**0.65**
I3	**–0.51**	0.14	0.20	**0.82**	–0.29	0.14	0.17		0.32	**0.62**	**0.94**	0.05	0.11	0.10
I4	–0.41	0.06	0.17	**–0.65**	–0.22	0.30	0.42	0.31		**0.83**	0.37	0.29	0.34	0.31
I5	**–0.66**	–0.06	0.14	**–0.85**	**–0.54**	0.29	0.43	**0.60**	**0.85**		**0.63**	0.28	0.38	0.35
I6	–0.49	0.17	0.25	**–0.82**	–0.27	0.18	0.21	**0.95**	0.38	**0.64**		0.04	0.08	0.06
I7	–0.30	–0.02	0.24	–0.40	–0.28	**0.50**	**0.52**	0.07	0.33	0.29	0.07		**0.99**	**0.98**
I8	–0.37	–0.05	0.24	–0.49	–0.37	**0.50**	**0.54**	0.15	0.39	0.41	0.14	**0.98**		**1.00**
I9	–0.35	–0.07	0.22	–0.48	–0.36	0.48	**0.51**	0.15	0.37	0.38	0.12	**0.97**	**0.99**	

[1] See text for explanation of variables. Coefficients in bold type are statistically significant at the 0.05 level.

not provide any important new information; mixed models will therefore not be discussed further.

ANALYSIS

Correlations Among Variables

Correlation coefficients (r) among variables indicate simple inter-relationships (Table 2). Number or bird species is significantly correlated with island area, latitude, and numbers of plant species. Thus, islands that are larger, are more northerly, and have a larger flora tend to support a larger number of bird species. In addition, there is a significant negative correlation with *I3* indicating a reduction in numbers of bird species with increased isolation as measured by average inter-island distance. Likewise a negative r occurs with the complement of number of islands or a mainland point within 100 miles (*I5*). For log data only there is in addition a significant r with elevation, indicating an increase in the log of numbers of bird species with topographic diversity as indicated by log elevation.

Number of plant species is significantly correlated with area and elevation. Islands that are larger and with greater topographic diversity seem to support larger floras. In addition, there is a significant negative r with *I5*, indicating, as with bird species, a tendency for an increase in numbers with an increase in the number of islands within 100 miles.

With regard to physical and geographic characteristics of the California Islands we find that larger islands rise to a greater maximum elevation. Thus, the larger islands tend to be topographically more diverse. The significant correlations between elevation and *I1* and *I2* indicate that islands with greater topographic relief also are those that tend to be farthest from a nearest neighbor. This relationship however is largely dominated by Guadalupe which rises well beyond most others and is by far the most distant island. Considering correlations with latitude, southerly islands seem to have a greater average distance from other islands (*I3*) and fewer islands or no mainland point within 50, 100, and 200 miles (*I4*, *I5*, and *I6*). Again these relationships are dominated by the conditions for Guadalupe.

It is also of interest to look at the interrelationships among the various isolation indices. *I1* and *I2* are logically correlated in that *I2*, distance to mainland or nearest intervening island, in half the cases contains the same values in *I1*, distance to mainland. *I4*, *I5*, and *I6*, complements of

numbers of islands or a mainland point within 50, 100, and 200 miles, are also correlated with one another because values for the categories of lesser distance figure into values for the categories of greater distance. Indices *I7*, *I8*, and *I9* are also highly intercorrelated. This is logical again in that values for the lower categories are figured into the higher categories and, in addition, contribute relatively more to the measure. Owing to the fact we are taking reciprocals of distances, the largest values will be those where distance is less. Thus the sum of reciprocals of distances of islands or a mainland point within 50 miles will contribute maximally, while reciprocals of distances for 100 and 200 mile categories will contribute proportionally less. This is reflected also in the correlations between *I1* and *I2* with *I7*, *I8*, and *I9*. Recall that the former two indices consider distance to mainland and distance to mainland or nearest intervening island, and note that all but one of these values is less than 50 miles. Finally, *I3* is correlated with *I5* and *I6* suggesting numbers of islands for the two greater distances figure strongly in the average distance measure of isolation.

Step-wise Regression Analysis

In order to isolate the components which figure most strongly in predicting variation in the numbers of land bird species (B) occurring during the breeding season on the California Islands, and correcting for correlations among the various factors, step-wise multiple regression analyses were carried out with B as the dependent variable and all other components as independent variables. The step-wist procedure admits independent variables into the regression model according to the degree of variation they explain in the dependent variable. For this analysis the "best" multiple regression equation will be taken as that which includes the fewest statistically significant partial regression coefficients and accounts for the greatest amount of variation in the dependent variable, i.e., has the highest multiple correlation coefficient. In the results to follow, statistical significance of partial regression coefficients is indicated by asterisks: $* \; 0.01 < p < 0.05$, $** \; 0.001 < p < 0.01$, $*** \; p < 0.001$. The percent of variation in the dependent variable explained by the simultaneous effect of independent variables in the regression equations is given in parentheses for each case.

The best simple and multiple regressions for numbers of bird species with untransformed data are

$$B = 5.14 + 0.055\,P^{***} \quad (73.8\%)$$
$$B = 17.03 + 0.050\,P^{***} - 0.053\,I3^{*} \quad (81.0\%)$$

With the admission of the next most important independent variable (*I4*) the relationships begin to deteriorate; only one partial regression coefficient remains significant and the percent of explained variation in B increases by a trivial amount. The equation is

$$B = 26.598 + 0.049\,P^{***} - 0.044\,I3 - 0.861\,I4 \quad (83.6\%)$$

Two independent variables appear to provide a better solution than do three.

With log transformed data the best simple and multiple regressions are

$$\log B = 0.027 + 0.520 \log P^{***} \quad (70.5\%)$$
$$\log B = 2.23 + 0.48 \log P^{***} - 1.005 \log I6^{*} \quad (78.4\%)$$

When the variable that explains the next greatest amount of variation in log B is admitted, again interpretation is made more difficult and the overall relationship is not substantially improved:

$$\log B = 4.82 + 0.45 \log P^{***} - 0.76 \log I6 - 1.16 \log I4 \quad (82.2\%)$$

Thus the best regression models are those with two independent variables and of these untransformed data provide the best statistical account of variation in numbers of bird species. The fact that *I3* appears as the second independent variable with untransformed data while *I6* appears as the

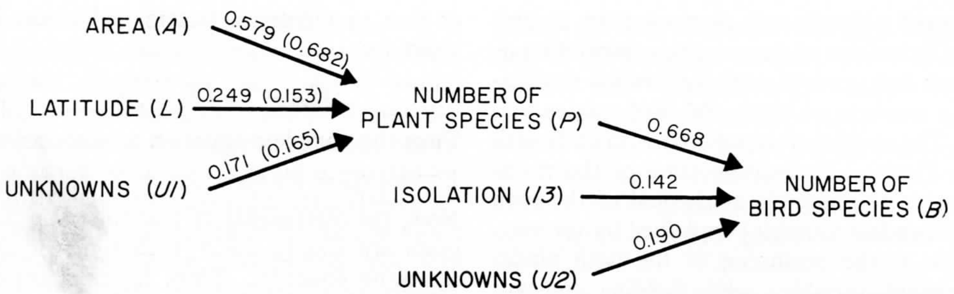

FIG. 2. Path diagram showing relationships among variables as indicated by step-wise multiple regression analysis. Numbers of bird species are explained by numbers of plant species, degree of isolation, and unknown factors. In turn, numbers of plant species are explained by island area, latitude, and unknown factors. Coefficients associated with each path are explained in the text. For numbers of plant species coefficients without parentheses are for untransformed data and values in parentheses are for log transformed data.

second independent variable with log data causes no special problem owing to the fact that these two variables are highly correlated (see Table 2) and likely measure very similar aspects of insular isolation.

Island area has figured predominantly in earlier work. However, in the present study area by itself is a relatively poor predictor of numbers. The results of simple regressions are

$$B = 10.11 + 0.11\,A^{*} \quad (32.6\%)$$
$$\log B = 2.01 + 0.21 \log A^{**} \quad (41.3\%)$$

The log transformed model provides a slightly better fit. One additional modification bears mentioning, namely that with deletion of numbers of plant species from the analysis. The multivariate results are

$$B = 30.99 - 1.91\,I5^{***} + 0.10\,A^{**} \quad (72.2\%)$$
$$\log B = -19.22 + 0.15 \log E^{***} + 5.24 \log L^{***} \quad (79.1\%)$$

It is evident that numbers of plant species is the single, most important predictor of numbers of bird species. Consequently it was of interest to delete B from the model and treat P as the dependent variable to determine those factors that statistically explain most of the variation in numbers of plant species. In this case the best simple and multiple regressions are

$$P = 81.54 + 2.14^{***}\,A \quad (55.7\%)$$
$$P = -844.39 + 2.22^{***}\,A + 29.09^{***}\,L \quad (82.9\%)$$

The next variable to enter the equation was E, elevation, but the associated partial regression coefficient is not quite statistically significant ($0.05 < p < 0.10$):

$$P = -698.48 + 3.49\,A^{***} + 25.24\,L^{**} - 0.05\,E \quad (86.5\%)$$

With log transformed data the results are

$$\log P = 3.73 + 0.45^{***} \log A \quad (71.8\%)$$
$$\log P = -14.74 + 0.42^{***} \log A + 5.36^{**}\,L \quad (83.5\%)$$
$$\log P = -14.74 + 0.49 \log A^{***} + 5.50 \log L^{**} - 0.22 \log I1 \quad (85.9\%)$$

It seems, therefore, that the log transformed model with two independent variables provides the best prediction of plant species diversity.

Path Diagram

From the foregoing we can see that island area and latitude account primarily for plant species numbers, while, in turn, plant species numbers and a measure of isolation account chiefly for numbers of bird species. For both plants and birds there are unknown factors that presumably will explain residual variation. This leads to construc-

tion of a simple path diagram (Fig. 2) and an estimation of the relative contribution of each independent variable toward explaining numbers of plant and bird species.

The coefficient associated with each path in Figure 2 is the proportion of the variation in the variable at the end of the path (dependent variable) explained by the variable at the beginning of the path (independent variable) while holding constant variation accounted for by other contributing variables. It is perhaps worthwhile to consider the calculation of the path coefficients in some detail. First, the standard partial regression coefficients (b'_i) are determined from the ordinary partial regression coefficients (b_i) by

$$b'_i = b_i \, (s_i/s_y)$$

where s_i is the standard deviation of the ith independent variable and s_y is the standard deviation of the dependent variable. The standard partial regression coefficient represents each variable in standardized form (mean = 0, s = 1) and is thus independent of the original units of measurement, whereas the value of each ordinary partial regression coefficient is not. For the multiple regression with numbers of bird species as the dependent variable $b'P = 0.778$ and $b'_{I3} = 0.280$. For numbers of plant species $b'_A = 0.776$ and $b'_L = 0.522$, and for the log transformed data $b'_{\log A} = 0.805$ and $b'_{\log L} = 0.345$.

In multiple regression analysis the multiple correlation coefficient ($R_{y,1\ldots k}$) is such that its square equals the proportion of variation in the dependent variable that is explained by the simultaneous effect of the independent variables. In addition we may write

$$R^2_{y,1\ldots k} = b'_1\, r_{y1} + b'_2\, r_{y2} + \ldots + b'_k\, r_{yk}$$

where r_{yi} is the correlation coefficient between the dependent variable and the ith independent variable and b'_i is the standard partial regression coefficient as described above. The residual variation, that is, variation in the dependent variable not accounted for by the independent variables or due to unknown factors and error, is given by

$$r^2_{yu} = 1 - R^2_{y,1\ldots k}$$

Thus the complete equation appears as

$$1 = b'_1\, r_{y1} + b'_2\, r_{y2} + \ldots + b'_k\, r_{yk} + r^2_{yu}$$

Now, the coefficients (C) of the path diagram are simply the $b'\ r$ elements of the foregoing equation. Thus, for numbers of bird species with untransformed data, and using b' calculated above and r from Table 2,

$$C_{BP} = b'_P\, r_{BP} = 0.668$$
$$C_{BI3} = b'_{I3}\, r_{BI3} = 0.142$$
$$C_{BU2} = 1 - C_{BP} + C_{BI3} = 0.190$$

Contribution coefficients for number of plant species with untransformed and log transformed data are calculated similarly.

Discussion and Conclusions

Statistical analysis supports a scheme to explain numbers of land bird species occurring during the breeding season on the islands off the coast of southern California and northwestern Baja California that involves a number of interacting variables. About 67% of the variation in numbers of bird species is explained by variation in the numbers of native plant species. An additional 14% of the variation is accounted for by isolation as measured by average inter-island distance, including in the average, distance to the nearest mainland point. The remaining 19% is attributable to unknown factors. In turn, 58% of the variation in numbers of plant species is explained by island area, 25% by latitude, and 17% by unknown factors. With log transformed data area contributes 68%, latitude contributes 15%, and unknown factors contribute 17% to variation in log P. Area by itself, in simple regressions, is a relatively poor predictor of bird species diversity, accounting for only 33% and 41% of the variation in numbers with untransformed and log transformed data, respectively.

The relationship between numbers of bird

ber. Compounding this, more isolated islands would also have a lower immigration rate of individuals of existing species, thus increasing the likelihood of extinction with small populations.

An isolation effect is particularly likely when we are dealing with resident and often strictly sedentary species, as many of the birds in this region are. Johnson (1972) has pointed out that certain species with low vagility are conspicuously absent from the California Islands even though seemingly suitable habitat is frequently available. Notably the Screech Owl (*Otus asio*), Nuttall's Woodpecker (*Dendrocopos nuttallii*), Wrentit (*Chamaea fasciata*), Plain Titmouse (*Parus inornatus*), California Thrasher (*Toxostoma redivivum*), and Brown Towhee (*Pipilo fuscus*) do not occur on the islands north of Los Coronados although common on the adjacent mainland. Diamond (1969) in a study of turnover on Los Coronados and the northern islands has discounted the importance of distance from the mainland in colonizations by birds in this region. However as Johnson has I believe correctly indicated, Diamond may not have considered the low vagility of many California species. Furthermore, distance from the mainland as in Diamond's study bears little on degree of isolation as I have measured it here; the correlation coefficient between *I1* and *I3* is near zero. Thus isolation may be an important factor while simple distance to the mainland is not.

Variation in island area by itself accounts for a significant but only a small portion of the variation in numbers of bird species. In combination with numbers of plant species and isolation, area is insignificant. In fact, as the path diagram shows, the only influence of area is indirectly through its accounting of numbers of plant species. However, as Greenslade (1968), MacArthur and Wilson (1967) and others have pointed out, as area is decreased there must come a point at which population sizes are so small that extinction rates are increased, and consequently equilibrium numbers of species are smaller. In general this is right, but it does not mean that these conditions are actually met in all archipelagos. Hamilton and Rubinoff (1967), for example, failed to find an area effect in the Galápagos Archipelago. The results of the present study strongly suggest that island area has an indirect, but not a direct, effect on bird species diversity in the California Islands. This view is supported by the data in Diamond (1969) which for the islands from Los Coronados northward show no relationship between island size and extinction rate. Perhaps only for the very smallest islands such as Todos Santos, San Martín, and San Gerónimo would populations be so small that extinction rate is elevated. But, even if this is true these three islands are so close to the mainland that replacement rates must be high.

The results for plant species diversity in the present study generally agree with those of Johnson et al. (1968) in a study that included the California Islands and South Farallon and Año Nuevo islands farther north. Log transformed models explain more variation in numbers than do untransformed data, although in the present study differences were slight. One of the major differences between my study and that of Johnson et al. is the inclusion in his results of *I1*, distance to the mainland, as a significant predictor of plant species diversity. Johnson employed a step-wise regression with numbers of native plant species for 14 islands (the island groups of Anacapa, Los Coronados, Todos Santos, and San Benito were excluded) and found significant partial regression coefficients with area, latitude, and distance to the mainland.

The larger islands in the California group clearly support a larger number of plant species than do the smaller islands. This may be due to the fact that larger islands provide larger targets for propagules and a greater diversity of sites for plant growth. Furthermore, the rate of extinction is probably higher on small islands. To a lesser degree latitude is an important factor, and

the significant inverse relationship with latitude can be explained in terms of climate. The more northerly islands receive a higher annual rainfall and the southern islands are more arid (Johnson et al., 1968). Thus, independent of island area, numbers of plant species are greater where rainfall is greater and are less where rainfall is reduced.

It has been aptly pointed out by MacArthur and Wilson (1967) that ecological (including biogeographical) theories are, like islands, stepping stones. Assessment of presumed causal pathways among faunistic and floristic diversity and a variety of environmental and geographic factors such as discussed here and as diagrammed in Figure 2, is a necessary refinement and a good step or two from the simple species-area relationships of earlier studies. We are still some distance though from a quantitative statement of the *real* relationships. Some obvious refinements would be to consider numbers of individuals as well as numbers of species and measure diversity in terms that take into account variation in both (e.g., information theory measures of diversity). Another aspect is to consider habitat diversity in terms that are ecologically more meaningful. For example, size, number and physical complexity of plant associations might have been more appropriate than plant species numbers in the present study, and would have been employed had the data been available. And, measures of isolation which are usually geographic distances or derivatives of distances may profitably incorporate wind and ocean currents and factors that affect dispersal. Mean wind velocity, for example, varies considerably among the northern islands. On San Nicholas, San Miguel, and Santa Rosa, nearly constant, high winds would have limiting effects on birds and plants and would tend to reduce certain dispersal or island-hopping patterns. Similarly, we may ask, should distance to a continent be weighted to take into account the fact that continents tend to be faunistically more rich than islands? And are not some source islands a richer source of colonizers than are others? What should the weighting factors be? And so on. It very quickly becomes clear that there is a continuing need for basic, descriptive papers on island biology, hopefully in numerical superiority to the synthetic and theoretical studies which must be based on solid data.

Summary

A model in the form of a path diagram is presented that attempts to explain statistically the numbers of land bird species breeding on the islands off the coast of southern California and northwestern Baja California, Mexico. Interrelationships among selected variables are investigated by step-wise multiple regression analysis.

With the present scheme numbers of bird species is largely accounted for by numbers of native plant species (67%). Secondarily, the degree of isolation, as measured by average inter-island distance (including in the average the distance to the nearest mainland point), and unknown factors account for the residual variation in numbers (14% and 19%, respectively). In turn, numbers of plant species is explained largely by island area (58% with untransformed data and 69% with log transformed data). Latitude also explains independently a significant portion of residual variation in plant species numbers (25% with untransformed data and 15% with log transformed data). The remaining variation is accounted for by unknown factors (17%). Island area is a relatively poor predictor of bird species diversity.

In terms of causal pathways, the present study indicates that coastal islands with floras that are more rich and possibly structurally more complex tend to support a larger avifauna. Furthermore, islands that are more isolated tend to have a lower equilibrial species number, which in accord with the equilibrium theory is due to reduced immigration rates and increased ex-

tinction rates. In addition, larger islands support a greater number of plant species, presumably because they provide a larger target for propagules, a greater diversity of sites for plant growth, and with larger populations have lowered extinction rates. Independent of area, a latitude effect suggests a relationship such that numbers of plant species increase with rainfall along the coast.

Acknowledgments

I have benefitted greatly from the comments of Drs. J. C. Barlow, J. B. Falls, R. I. C. Hansell, and J. D. Rising, all of who I thank for their time in discussing the manuscript. Ms. C. M. Goodwin prepared the illustrations. Computer time was made available by the Royal Ontario Museum. This research was carried out with the support of a grant from the National Research Council of Canada (No. A-4901).

Literature Cited

Crowell, K. L. 1962. Reduced interspecific competition among the birds of Bermuda. Ecology 43:75–88.

Diamond, J. M. 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. Proc. Nat. Acad. Sci. 64:57–63.

Grant, P. R. 1966. Ecological compatibility of bird species on islands. Amer. Natur. 100:451–462.

Greenslade, P. J. M. 1968. Island patterns in the Solomon Islands bird fauna. Evolution 22:751–761.

Grinnell, J. 1928. A distributional summation of the ornithology of Lower California. Univ. California Publs. Zool. 32:1–300.

Grinnell, J., and A. H. Miller. 1944. The distribution of the birds of California. Pacific Coast Avif. no. 27. 608 pp.

Hamilton, T. H., and N. E. Armstrong. 1965. Environmental determination of insular variation in bird species abundance in the Gulf of Guinea. Nature 207:148–151.

Hamilton, T. H., R. H. Barth, Jr., and I. Rubinoff. 1964. The environmental control of insular variation in bird species abundance. Proc. Nat. Acad. Sci. 52:134–140.

Hamilton, T. H., and I. Rubinoff. 1967. On predicting insular variation in endemism and sympatry for the Darwin Finches in the Galápagos Archipelago. Amer. Natur. 101: 161–171.

Howell, T. R., and T. J. Cade. 1954. The birds of Guadalupe Island in 1953. Condor 56:283–293.

Johnson, M. P., L. G. Mason, and P. H. Raven. 1968. Ecological parameters and plant species diversity. Amer. Natur. 102:297–306.

Johnson, N. K. 1972. Origin and differentiation of the avifauna of the Channel Islands, California. Condor 74:295–315.

Lack, D. 1969. Subspecies and sympatry in Darwin's Finches. Evolution 23:252–263.

MacArthur. R. H. 1964. Environmental factors affecting bird species diversity. Amer. Natur. 98:387–397.

MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution 17:373–387.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N.J. 203 pp.

MacArthur, R., H. Recher, and M. Cody. 1966. On the relation between habitat selection and species diversity. Amer. Natur. 100:319–332.

Miller, A. H. 1951. A comparison of the avifaunas of Santa Cruz and Santa Rosa Islands, California. Condor 53:117–123.

Philbrick, R. N. (ed.). 1967. Proceedings of the symposium on the biology of the California Islands. Santa Barbara Botanic Garden, Santa Barbara, Calif. 363 pp.

Preston, F. W. 1962. The canonical distribution of commonness and rarity: part 1. Ecology 43:185–215.

Thorne, R. F. 1969. The California Islands. Ann. Missouri Bot. Gard. 56:391–408.

Thornton, I. B. 1967. The measurement of isolation on archipelagos, and its relation to insular faunal size and endemism. Evolution 21:842–849.

Watson, G. E., III. 1964. Ecology and evolution of passerine birds on the islands of the Aegean Sea. University Microfilms, Ann Arbor, Michigan. 456 pp.

Appendix

Land bird species breeding on the California Islands, excluding large raptors and recently introduced species. Data from Grinnell (1928), Grinnell and Miller (1944) and Howell and Cade (1954).

Species	Island Number[a]															
	1	2[b]	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Falco sparverius	x	x	x	x	x	x	x	x	x	x			x	x		x
Lophortyx californicus							x									
Zenaidura macroura		x	x				x	x								
Tyto alba		x	x	x					x	x	x					x
Speotyto cunicularia	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x
Asio otus							x	x								
Chordeiles acutipennis						x										
Aëronautes saxatalis	x	x	x	x	x	x	x	x	x	x			x			
Calypte costae						x								x	x	
Calypte anna								x	x	x			x		x	
Selasphorus sasin		x	x	x			x	x	x	x			x		x	
Megaceryle alcyon			x													
Colaptes cafer			x		x		x						x			
Melanerpes formicivorus			x													
Myiarchus cinerascens										x						
Sayornis nigricans		x	x				x	x		x						
Sayornis saya															x	
Empidonax difficilis		x	x				x	x								
Eremophila alpestris	x	x	x	x	x	x	x	x								
Hirundo rustica			x	x		x	x	x	x							
Aphelocoma coerulescens			x													
Corvus corax	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x
Psaltriparus minimus			x				x									
Sitta canadensis			x										x			
Thryomanes bewickii		x	x	x			x	x					x		x	
Salpinctes obsoletus	x	x	x	x	x	x	x	x	x	x	x		x	x	x	
Mimus polyglottos		x	x				x	x							x	
Regulus calendula													x			
Lanius ludovicianus		x	x	x			x	x								
Vireo huttoni		x	x				x									
Vermivora celata	x	x	x	x		x	x	x	x	x						
Geothlypis trichas									x							
Sturnella neglecta	x	x	x	x	x	x	x	x								
Icterus cucullatus							x								x	
Carpodacus mexicanus	x	x	x	x	x	x	x	x	x	x			x	x	x	
Spinus psaltria		x	x				x									
Spinus lawrencia			x				x									
Pipilo erythrophthalmus		x	x				x	x					x			
Passerculus sandwichensis										x				x		
Chondestes grammacus			x													
Aimophila ruficeps			x	x			x[c]			x						
Amphispiza bilineata															x	x
Amphispiza belli					x			x			x					
Spizella passerina		x	x				x	x								
Melospiza melodia	x	x	x	x		x		x	x							

[a] In order, island names are: 1, San Miguel; 2, Santa Rosa; 3, Santa Cruz; 4, Anacapa; 5, San Nicholas; 6, Santa Barbara; 7, Santa Catalina; 8, San Clemente; 9, Los Coronados; 10, Todos Santos; 11, San Martín; 12, San Gerónimo; 13, Guadalupe; 14, San Benito; 15, Cedros; and 16, Natividad.

[b] Sight records of *Aimophila ruficeps* and *Amphispiza belli* on Santa Rosa Island have been discredited (Miller 1951: 119).

[c] Not reported since 1863 (Grinnell and Miller 1944: 497).